Reference: *Biol. Bull.* **172:** 161–177. (April, 1987)

SEXUAL REPRODUCTION AND COLONY GROWTH IN THE SCLERACTINIAN CORAL *PORITES ASTREOIDES*

ELIZABETH A. CHORNESKY[1,2] AND ESTHER C. PETERS[2]

[1]*Department of Biology and Stone Harbor Marine Laboratory, Williams Hall, Lehigh University, Bethlehem, Pennsylvania 18015*, and* [2]*Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560*

Abstract

This study examines patterns of sexual reproduction and colony growth for *Porites astreoides* Lamarck, an abundant Caribbean reef coral. Five factors influence the reproductive condition of this coral in Jamaica: (i) Season, (ii) lunar day, (iii) polyp location within a colony, (iv) colony size, and (v) colony age. *P. astreoides* has an unusual mixed breeding system: Approximately half of colonies are hermaphroditic and half are female. Although gonads occur in some colonies throughout the year, there are clear seasonal differences both in the number of reproductive colonies within the population and in colony fecundity. Male gametes are spawned monthly around the time of the full moon. The abundance and maturity of brooded larvae peaks prior to the new moon. Within reproductive colonies, gonads and brooded larvae are more abundant in central polyps than at colony edges. Among female colonies, the onset of reproduction is apparently related to colony size, whereas the fecundity of individual polyps is related to colony age. Hermaphroditic and female colonies differ in the size at which most colonies are reproductive. Rates of vertical and lateral growth for *P. astreoides* increase with colony size, but not with colony age. These findings demonstrate how the combined effects of several variables can cause individuals within a population to differ greatly in reproductive condition, fecundity, and growth rate.

Introduction

Since the turn of the century, there have been numerous descriptions of the patterns of reproduction and growth among reef corals (*e.g.,* Duerden, 1902; Wood-Jones, 1910; Vaughan, 1915; Marshall and Stephenson, 1933; Atoda, 1947; Harrigan, 1972; Connell, 1973; Loya, 1976; Gladfelter *et al.,* 1978; Stimson, 1978; Rinkevich and Loya, 1979a, b; Hughes and Jackson, 1980, 1985; Goreau *et al.,* 1981; Kojis and Quinn, 1981, 1982; Harriott, 1983; Highsmith, 1982; van Moorsel, 1983; Babcock, 1984; Harrison *et al.,* 1984; Jokiel *et al.,* 1985; Shlesinger and Loya, 1985; Stoddart and Black, 1985; Szmant-Froelich *et al.,* 1985; Wallace, 1985; Kinzie and Sarmiento, 1986; Szmant, 1986). It is becoming clear from some of these studies that co-occurring colonies of a given species can differ greatly in important characteristics such as reproductive state, fecundity, and growth rate (Marshall and Stephenson, 1933; Connell, 1973; Stimson, 1978; Rinkevich and Loya, 1979a, b; Harriott, 1983;

Received 14 April 1986; accepted 30 January 1987.
* Address for correspondence.

Kojis and Quinn, 1981, 1984, 1985; Hughes and Jackson, 1985; Stoddart and Black, 1985; Szmant-Froelich, 1985; Wallace, 1985).

Such variation can be caused by external events such as environmental stress. For example, coral fecundity may decline due to injury (Kojis and Quinn, 1981), exposure to sedimentation or turbidity (Kojis and Quinn, 1984), or competitive encounters (Rinkevich and Loya, 1985). Similarly, rates and patterns of coral growth may be affected by colony breakage (Loya, 1976).

Other intraspecific differences in reproduction and growth are more inherent to populations, resulting from relatively predictable factors such as ontogenetic stage, season, or lunar period. For example, in protandrous hermaphroditic species, small and/or young colonies are male while larger and/or older colonies are hermaphroditic (Rinkevich and Loya, 1979a; Kojis and Quinn, 1981). Among species in which the onset of reproduction is related to colony size, including certain gorgonian octocorals (Wahle, 1983) and scleractinian corals (Rinkevich and Loya, 1979b; Kojis and Quinn, 1981, 1985; Babcock, 1984; Szmant-Froelich, 1985), mature colonies will stop producing gametes when reduced in size below the reproductive threshold value, irrespective of their age (Wahle, 1983; Kojis and Quinn, 1985; Szmant-Froelich, 1985). Polyp fecundity has been shown to vary with colony size (Rinkevich and Loya, 1979b; Kojis and Quinn, 1981; Babcock, 1984), with colony age (Kojis and Quinn, 1985), with polyp size (Harriot, 1983), and with polyp location within a colony (Harrigan, 1972; Rinkevich and Loya, 1979b; Wallace, 1985). Finally, both the abundance and developmental stage of coral gonads or brooded larvae can change temporally with season or with lunar period (*e.g.*, Harriot, 1983; Kojis and Quinn, 1984; Stoddart and Black, 1985).

When individuals of a species vary greatly, estimates of reproductive condition, fecundity, or growth rate based on small sample sizes may not accurately reflect patterns of reproduction and growth within the population as a whole. Furthermore, interspecific comparisons may be problematic when intraspecific differences equal or exceed those occurring between species. Nevertheless, remarkably few studies have systematically evaluated the levels and possible sources of intraspecific variation in reproduction or growth (*e.g.*, Connell, 1973; Rinkevich and Loya, 1979b; Kojis and Quinn, 1981, 1984, 1985; Harriot, 1983; Babcock, 1984; Hughes and Jackson, 1985; Szmant-Froelich, 1985; Kinzie and Sarmiento, 1986).

This paper documents intraspecific patterns of sexual reproduction and growth within a population of the reef coral *Porites astreoides* Lamarck. Specifically, we describe: (i) Seasonal and lunar patterns in sexual reproduction; (ii) intra-colony variation in polyp fecundity and gender; (iii) the effects of colony age on polyp fecundity; (iv) the relationship between colony size and reproductive condition; and (v) changes in colony growth rate that occur with increasing colony size.

Materials and Methods

Study organism

Porites astreoides is among the most common corals on many Caribbean reefs and occurs over a wide range of depths and habitats (Goreau, 1959; Goreau and Wells, 1967). It is generally considered to be among the most fecund species, since juveniles appear early and abundantly in studies of coral recruitment (Bak and Engel, 1979; Rylaarsdam, 1983; Rogers *et al.*, 1984). *P. astreoides* colonies grow in encrusting, platey, and mound-like morphologies. Corals sampled in this study had encrust-

ing to plate-like shapes, as these predominate in the study population at −10 m on the west forereef of Discovery Bay, Jamaica. At this site, instances where injury has subdivided coral colonies into physiologically separate, but genetically identical "daughter" colonies (Hughes and Jackson, 1980, 1985) were usually clearly identifiable by the color similarity, close proximity, or remaining skeletal connections between adjacent colonies. Previous surveys suggest that most colonies (78%) in this population result from the independent recruitment of larvae rather than from the subdivision of larger colonies (Chornesky, unpub. data).

Sexual reproduction

Sexual reproduction was evaluated between October 1981 and July 1982 by histologically examining coral tissues for gonads and larvae. Our sampling scheme was designed to reveal both seasonal and lunar patterns in reproductive periodicity. Tissues were sampled throughout one lunar period (28 days) during each of four months that reflect the annual range of seawater temperature: July (high); January (low); April (intermediate, increasing); and October (intermediate, decreasing). During each of these four months, samples were collected every five or six days (a total of five sampling days per month). On each sampling day, separate tissue specimens of thirty or more polyps were collected from both the centers and growing edges of five *P. astreoides* colonies. Colonies sampled on any given day were spatially separated by distances of several meters, and thus can be safely assumed to be of different genotypes. Individual colonies were sampled only once during the study, to avoid any adverse effects of repeated injury on coral reproduction (*e.g.,* Kojis and Quinn, 1981). In total, 100 colonies were sampled (4 months × 5 days × 5 colonies).

The general condition, size, and maximum skeletal thickness of each colony was recorded. Colony size was determined by calculating the surface area of live coral tissues (the area of an ellipse defined by the two largest, perpendicular diameters laid across the colony's living tissues). Maximum skeletal thickness was measured when possible (59% of colonies sampled).

For encrusting and plate-shaped corals, maximum thickness provides a better measure of colony age than surface area. Surface area is often only poorly correlated with colony age since injury along colony perimeters frequently interrupts or inhibits the lateral expansion of corals (Jackson, 1979; Hughes and Jackson, 1980, 1985). In contrast, colony centers are less likely to be injured and upward skeletal growth in this region may proceed relatively uninterrupted. The growth discrepency between colony regions is often reflected in colonies of equal maximum thickness but widely varying surface area (Chornesky, unpub. data). Thus, maximum skeletal thickness is the most reliable historical marker of previous growth, and is used here to estimate minimum colony age.

Results of tests for size differences of sampled corals among sampling days and among sampling months by one-way ANOVA were non-significant (among days, $F = .98$, $P > .25$, $df = 19,80$; among months, $F = .18$, $P > .75$, $df = 3,96$). Similarly, colony thickness did not differ significantly among sampling months ($F = .77$, $P > .5$, $df = 3,58$). The numbers of colonies for which thickness could be measured did not allow for statistical comparison among sampling days. Colony size and thickness were not significantly correlated for the population of corals sampled ($r = .22$, $P > .05$).

To minimize the potential effects of uncontrolled interactions and events, we deliberately sampled colonies with few contacts along their borders with adjacent ani-

mals, and with no evidence of disease, lesions, bare spaces, or other injury. Pieces of corals were broken off *in situ* using a chisel. Specimens were kept immersed in seawater, and then fixed in Helly's fixative within two hours of collection. Fixed tissues were decalcified using a solution of dilute HCl and EDTA and stored in 70% ethanol (Peters, 1984). Specimens were subsequently embedded in Paraplast (Sherwood Medical) and sectioned at 6 μm. The resulting slides were stained either with hematoxylin and eosin or with Heidenhain's Aniline Blue Method (Luna, 1968). Three slides were made at different depths within each specimen, one each from the top, middle, and bottom thirds of the tissues. Longitudinal sections of polyps were also prepared when possible.

On each cross-section of tissues, the abundance and condition of eggs, spermaries, and developing larvae were quantified by surveying 10 separate, non-overlapping fields at 125× magnification. Fields contained three to four polyps ($\bar{x}$ = 3.7, S.D. = .71, no. fields counted = 79). Developmental stages of gonads and larvae were estimated by size and morphology (Fig. 1A-F, I). Statistical comparisons between central and peripheral tissues included data from slides cut from mid-depth in the tissues. All other statistical analyses (Sokal and Rohlf, 1969; Steele and Torrie, 1960) were performed on data from the slide of each specimen that revealed the maximum number of gonads.

Growth rate

Growth rates for *P. astreoides* colonies were determined by staining colonies *in situ* with the vital stain Alizarin red S (*e.g.,* Dodge *et al.,* 1984). Alizarin red S is incorporated into a thin layer of skeleton during staining and provides a marker for measuring subsequent skeletal growth. In May of 1981, 10 colonies between 6 and 300 cm^2 were enclosed for 24 h in clear plastic bags containing a small amount of stain. Stained corals appeared to be healthy and lacked any evidence of injury or contacts with other sessile animals along their borders. After one year of growth, the colonies were collected and cut in half. Vertical growth was measured at five random locations along the cut face, and lateral growth was measured where five randomly chosen radii intersected the colony perimeter.

Results

Each factor examined—season, lunar day, polyp location, colony size, and colony age—influenced some aspect of reproduction or growth in *Porites astreoides.* The resulting patterns are complex; therefore, we have summarized the major findings of the results in Table I.

Breeding system

Gender and reproductive state of colonies. Colonies of *P. astreoides* were either female or hermaphroditic. Of the 100 colonies sampled, 28% contained only female gonads, 26% contained both male and female gonads, and 43% contained no gonads. The only colony having exclusively male gonads contained only a single spermary. Thus, the existence of unisexual males in this population is doubtful. Brooded larvae were observed in 50% of female colonies and in 46% of hermaphroditic colonies.

Distribution of gender among and within polyps. Within hermaphroditic colonies, individual polyps could be either male, female, or hermaphroditic. The proportions of these three polyp types varied among colonies. Within hermaphroditic polyps,

TABLE I

Summary of results

A. BREEDING SYSTEM
   1. *Gender:* 52% female, 48% hermaphroditic
   2. *Fertilization:* Internal; larvae brooded
B. TIMING OF REPRODUCTION
   1. *Seasonal:* Peaks during April
   2. *Lunar:* Spermaries spawned around time of full moon; larvae mature prior to new moon
C. FACTORS AFFECTING POLYP FECUNDITY
   1. *Location within a colony:* Centers more fecund than colony edges
   2. *Colony size:* Associated with onset of female reproduction
   3. *Colony age:* Correlated with polyp fecundity in females
D. FACTORS AFFECTING COLONY GROWTH
   1. *Colony size:* Correlated with vertical and lateral growth rates

male and female gonads were occasionally found on the same mesentery (Fig. 1D, E). In both female and hermaphroditic colonies, gonads did not appear restricted to any particular mesenteries, although they were most frequent on incomplete mesenteries (Fig. 1H). Up to nine mesenteries might contain gonads within any given polyp.

Cross and longitudinal sections of mesenteries yielded similar counts of one or, rarely, two to three eggs per mesentery. In contrast, cross-sectional counts of spermaries could underestimate actual spermary abundance. Mesenteries in cross-section contained one to three spermaries. However, up to 14 spermaries, arranged vertically and occasionally overlapping, might be visible in longitudinal sections of mesenteries (Fig. 1E). There was no pattern to the vertical distribution of male and female gonads within hermaphroditic mesenteries (Fig. 1E).

Location of gonads within colonies

Centers versus *edges.* Gonads were not distributed evenly throughout colonies. Comparison of central and peripheral tissues showed that the densities per polyp of both eggs and spermaries were greatest at colony centers (one-tailed, paired *t*-tests: For eggs, $P = .005$; for spermaries, $P = .016$). Brooded larvae were too rare to perform a statistical test of the relationship between abundance and position within colonies, but appeared to follow the same trend.

Within centers. The distribution of gonads among central polyps was patchy. In reproductive colonies, on average only half (51%) of the 10 fields surveyed in each central slide contained gonads (no. slides surveyed = 153).

Within edges. Due to the low density of gonads at colony edges, gender might easily be misidentified from samples of only peripheral polyps. Sixty-one percent of hermaphroditic colonies lacked male, female, or both types of gonads in peripheral polyps. Similarly, 36% of female colonies lacked eggs in peripheral regions. Only one of the 54 reproductive colonies contained gonads in peripheral tissues of a type (male) that was absent in the central tissues.

Development of gametes and larvae

Female and male gamete development were divided into three approximate stages (early, middle, and late; Fig. 1).

Female. The earliest recognized female gametes had a basophilic cytoplasm and

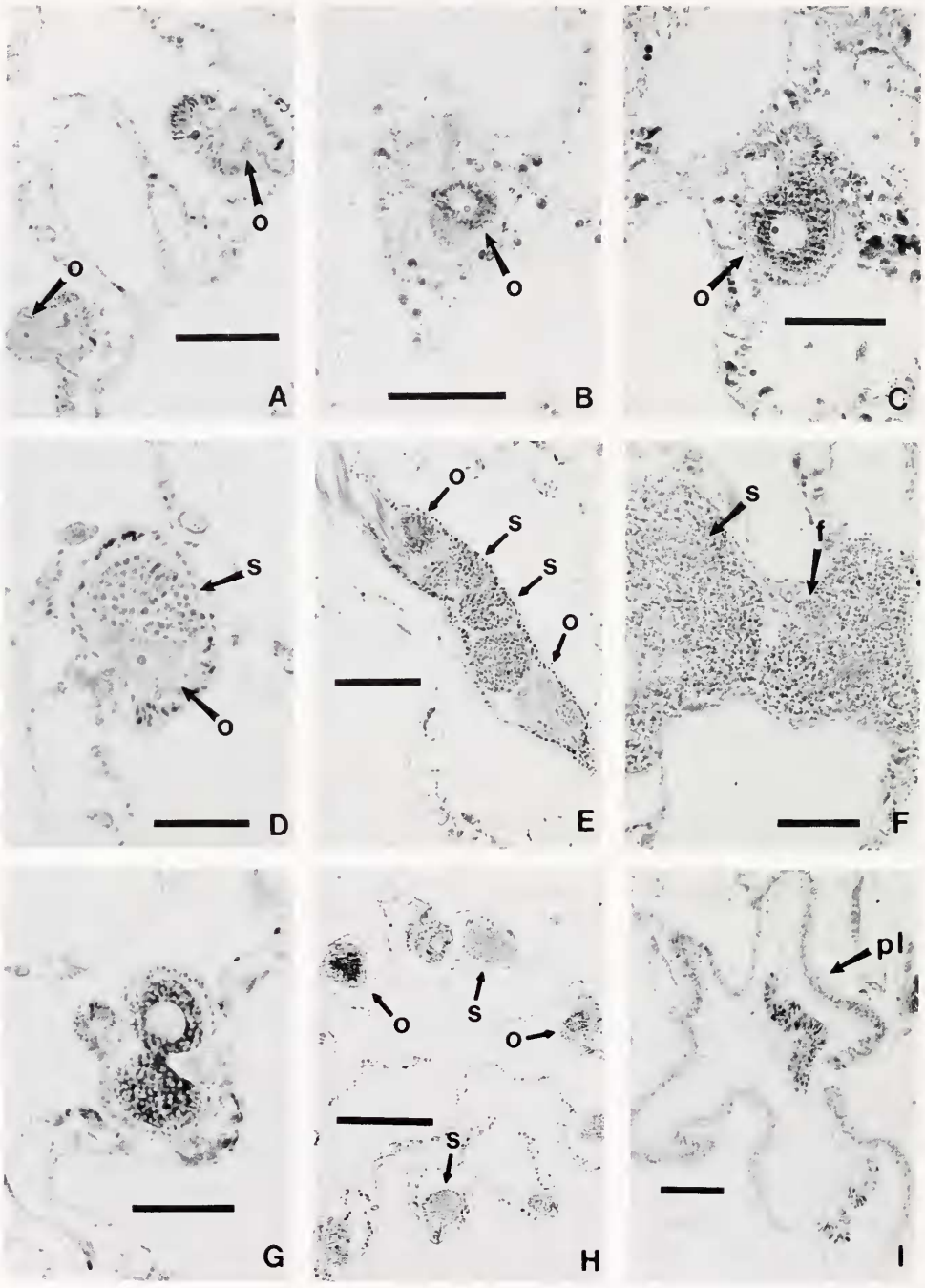

FIGURE 1. Gonad and larval development in *Porites astreoides*. A. Early female gametes (o) developing in two mesenteries. B. Later in development, the cytoplasm of oocytes changes in staining characteristics, and lipid droplets accumulate. C. Mature egg (o). Diameters of released eggs were between 130 and 170 μm in histological sections. D. Rare view of early oocyte (o) and spermary (s) developing on the same

an enlarged nucleolus. Initially present in the gastrodermis, the oocytes were later enveloped in the mesoglea (Fig. 1A). Mid-stage oocytes were larger and eosinophilic, with lipid droplets in the yolk (Fig. 1B). They had a distinctive eccentric nucleus and prominent nucleolus, and were surrounded by a thin layer of mesoglea. Mature eggs had completed vitellogenesis (Fig. 1C). Occasionally, eggs assumed a "dumbell" shape, with the nucleus in one lobe (Fig. 1G). Serial sections suggested that this unusual shape was a fixation artifact (but see Szmant-Froelich *et al.*, 1985).

Male. Male gametes developed from rounded interstitial cells with a large nucleus and little cytoplasm. These cells were found in the gastrodermis, although early spermatogonia were surrounded by mesoglea (Fig. 1D). Mid-stage spermaries were distinguished by the enlargement of irregularly shaped nests of cells with occasional mitotic figures visible (Fig. 1E). Later spermaries contained smaller spherical secondary spermatocytes and spermatids. Mature follicles were quite large, and stretched the mesenteries so that they were covered by only a layer of squammous gastrodermal cells and associated mesoglea (Fig. 1F). Mature spermatozoa with eosinophilic tails appeared first in follicle centers and eventually filled them completely. Spermatozoa appeared to burst from mesenteries, and large masses were found in polyp coelenterons and gastrovascular canals. Remnants of spermatozoa occurred in some mesenteries following spawning, occasionally accompanied by redeveloping spermaries.

Larvae. Fertilization for *P. astreoides* is internal. Mature eggs were observed being extruded between gastrodermal cells in mesenteries, and masses of sperm were seen surrounding released eggs in the coelenterons of several colonies. While most embryos were found in polyp coelenterons and gastrovascular canals, one appeared to lie within a mesentery, as observed by N. I. Goreau in Caribbean *Porites* spp. (Fadlallah, 1983). Early developing embryos consisted of numerous round blastomeres with external red granular yolky cells (Heidenhain's-stained) and a vacuolated central area. Zooxanthellae apparently invaded the endoderm of embryos as tissue layers differentiated. In later embryos, the interior was filled with foamy endodermal cells, and chromophore (lipofuchsintype pigment) cells and nematocysts appeared in the ectoderm. The most mature brooded planulae had six mesenteries, a well-formed stomodaeum, and embryonic chromophore cells and nematocysts in both the ectoderm and endoderm (Fig. 1I).

The timing of reproduction

Reproductive events for *P. astreoides* occurred with both seasonal and lunar periodicities. The following analyses of reproductive patterns include only data from colony centers, since they provide the most reliable estimate of colony gender and fecundity.

Seasonal periodicity. Although gonads and larvae were present in at least some

---

mesentery. Primary spermatogonia were 4–6 μm in diameter. E. Longitudinal section of mesentery containing two oocytes and six spermaries. F. Mature spermaries (s), as tails on spermatozoa begin to appear. A new follicle (f) is also beginning to develop. Individual spermatozoa had 1.5–2 μm triangular-shaped heads. G. "Dumbbell" shaped egg in mesentery. H. Cross-section through a polyp showing arrangement of eggs (o) and spermaries (s). I. Section through mature planula (pl) with six mesenteries and early filament tissues. Scale bars in A, B, C, E, F, and G, all equal 100 μm. Scale bar in D = 50 μm, and in H and I = 200 μm. Photomicrographs were taken using a Zeiss Photomicroscope II, and eggs and sperm were measured using a calibrated ocular micrometer under an oil immersion objective.

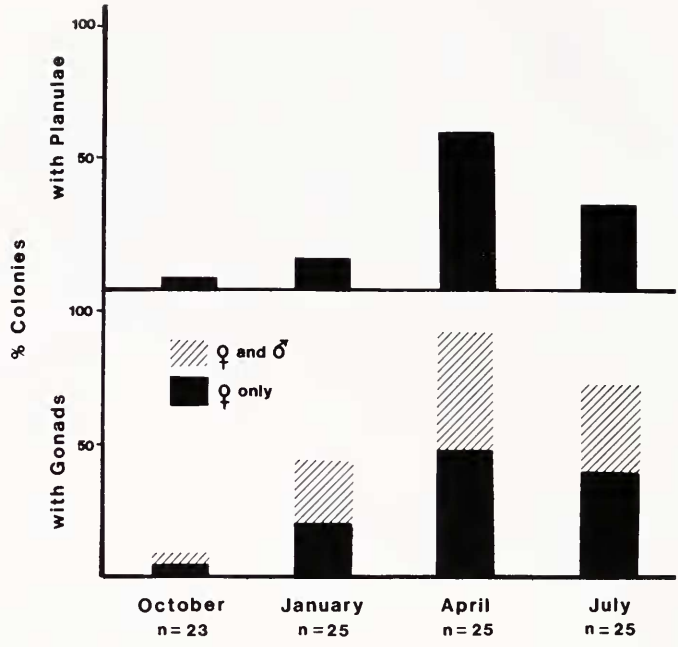

FIGURE 2. Seasonal variation in the proportion of colonies containing gonads or planula larvae.

colonies throughout the year (Fig. 2), there was a clear association between season and the numbers of colonies containing either gonads ($\chi^2 = 37.6$, df = 3, $P < .005$) or developing larvae ($\chi^2 = 22.67$, df = 3, $P < .005$). The maximum number of reproductive colonies occurred during April. Due to the low reproductive activity in October (2 colonies), analyses of reproductive patterns that follow compare only January, April, and July.

Among reproductive colonies, polyp fecundity varied seasonally (Table II). For both female and hermaphroditic colonies, the density of eggs in tissues differed among sampling months (Kruskal-Wallis comparisons: For females—H = 6.82, df = 2, $P < .05$; for hermaphrodites—H = 6.65, df = 2, $P < .05$). In particular, more ova were observed in April samples than in July (two-tailed, Mann-Whitney: For females—U = 97, n1 = 12, n2 = 10, $P < .02$; for hermaphrodites—U = 73, n1 = 11, n2 = 8, $P < .02$). Similarly, numbers of developing larvae also varied among months (Kruskal Wallis H = 80.4, df = 2, $P < .005$), with the highest values occurring during April. Interestingly, the numbers of male gonads in hermaphroditic colonies did not appear to vary seasonally (Kruskal-Wallis: H = 3.55, df = 2, $P > .1$).

Lunar periodicity. Superimposed upon the seasonal changes in reproduction was a pronounced lunar periodicity (Fig. 3). Most spermaries were mature prior to the full moon, and immature spermaries were most common between the full and new moons (Fig. 3A). In contrast, egg development showed no clear lunar pattern (Fig. 3B). Male and female gonadal abundance did not vary predictably with lunar day. Both the abundance (Fig. 3C) and maturity of brooded larvae peaked prior to the new moon.

TABLE II

Seasonal variation in the density of gonads and developing larvae in tissues of Porites astreoides*

	Female colonies		Hermaphroditic colonies		
	Eggs	Larvae	Eggs	Spermaries	Larvae
Oct.**	.08	0.0	.03	.43	0.0
Jan.	.40	0.0	.57	.20	0.0
	(.22–1.7)	(0.0–.03)	(.08–1.9)	(.05–.54)	(0.0–.08)
April	.51	.07	.38	.20	.03
	(.05–2.3)	(0.0–.43)	(.14–.78)	(.05–1.5)	(0.0–.62)
July	.18	0.0	.09	.07	.01
	(.03–.59)	(0.0–.03)	(.03–.54)	(.03–.73)	(0.0–.14)

* Values presented as median number observed per polyp and the (range).

** No ranges given since only one female and one hermaphroditic colony were observed during October.

Differences among colonies

Gender. Reproductive state was significantly associated with colony size for corals sampled during January, April, and July ($\chi^2 = 13.25$, df = 4, $P < .01$) (Fig. 4). Although the proportion of hermaphroditic colonies remained constant for all size classes, the proportion of non-reproductive colonies declined and the proportion of female colonies increased with increasing size class (Fig. 4). These trends suggest that hermaphroditic colonies are reproductive at relatively small sizes, whereas small colonies lacking gonads are females that will become reproductive when they increase in size. The presence of both females and hermaphrodites among the smallest colonies sampled (7 cm diameter, 38 cm^2), however, suggests that some unknown factor(s), in addition to size, may also influence the onset or continuation of female reproduction. Gender and reproductive state were not significantly associated with colony age (thickness).

Fecundity. Mean polyp fecundity differed widely among colonies (Table II, range values). To examine the potential sources for this variation, we compared the fecundity of all colonies of known size and age (thickness) from the April collecting period. This subsample was chosen because: (1) April was the month when the maximum number of colonies was reproductive and reproductive colonies were the most fecund; (2) gonadal abundance did not vary over a lunar period, allowing comparison among colonies sampled on different lunar days; and (3) previous studies have suggested that colony size (Kojis and Quinn, 1981; Babcock, 1984) and/or colony age (Rinkevich and Loya, 1979b; Kojis and Quinn, 1985) may influence the fecundity of coral polyps.

The potential influences of colony size and age (thickness) on fecundity were separated statistically by calculating partial correlation coefficients (Steele and Torrie, 1960). This is equivalent to calculating the correlation between fecundity and size while holding age constant (fs·a), and calculating the correlation between fecundity and age while holding size constant (fa·s).

Female colonies showed no significant correlation between fecundity and colony size ($r_{fs \cdot a} = -.35$, n = 9, $P > .05$). In contrast, female fecundity was significantly correlated with colony age (thickness) ($r_{fa \cdot s} = .91$, n = 9, $P < .01$), in part due to the

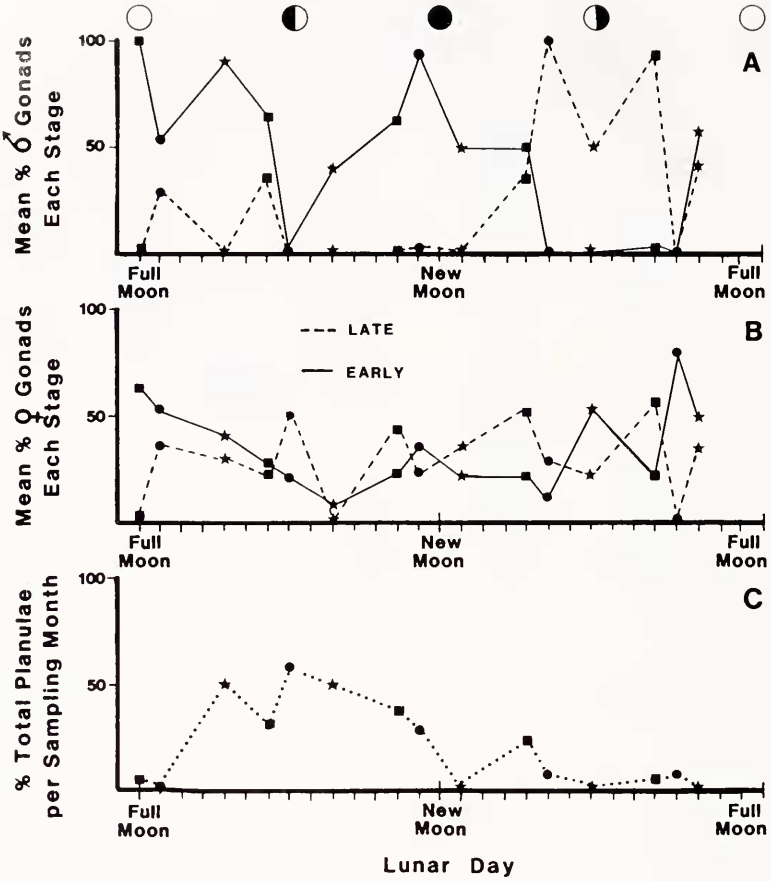

FIGURE 3. Lunar periodicity of reproduction in *Porites astreoides*. A. Lunar changes in the frequency of early (solid line) and late (dashed line) male gonads. Mature spermaries were most abundant prior to the full moon, and immature spermaries were most abundant between the full and new moons. B. Frequencies of immature (solid line) and mature (dashed line) eggs *versus* lunar day. There was no clear lunar pattern in the development of eggs. In both A and B, data are reported as the mean percent per colony of each stage. C. Most of the larvae observed were in tissues collected between the full and new moons. Figure presents data for January (stars), April (squares), and July (dots) sampling periods.

occurrence of a highly fecund small (212 cm^2) but old (6.5 cm thick) colony within the sample population (Fig. 5).

For hermaphroditic colonies, none of the partial correlations between either colony size or colony age (thickness) and any of three measures of fecundity—eggs per polyp, spermaries per polyp, or (eggs + spermaries) per polyp—was significant (for all six partial correlations, $.45 > r > -.51$, $P > .05$, $n = 9$). Similarly, the ratio of male:female gonads within hermaphroditic colonies (i) was not significantly correlated with either colony size ($r_{is \cdot a} = -.31$, $P > .05$) or colony age (thickness) ($r_{ia \cdot s} = .45$, $P > .05$).

Growth rate

We examined two measures of growth: Lateral extension of the growing edge and vertical deposition of new skeletal material over the pre-existing skeleton (Fig. 6). The

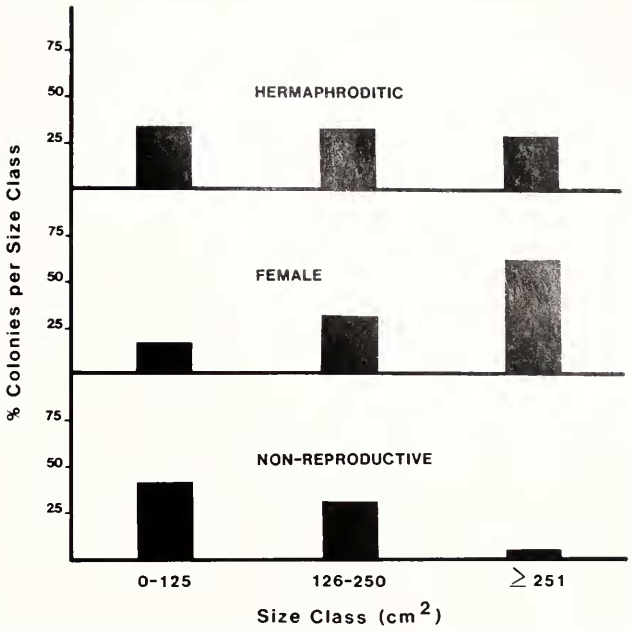

FIGURE 4. The relationship between gender and colony size. Colonies smaller than 125 cm^2 in surface area were mostly non-reproductive or hermaphroditic. With increasing size, the proportion of female colonies increased while that of non-reproductive colonies decreased. The frequency of hermaphroditic colonies remained approximately equal for all three size classes.

median rate of lateral growth was .73 cm/year (range = .2–1.8). The median rate of vertical growth was .31 cm/year (range = .13–.46).

Partial correlation coefficients were calculated to separate the potential influences of colony size and colony age (thickness) on growth rates. Rates of both vertical (v)

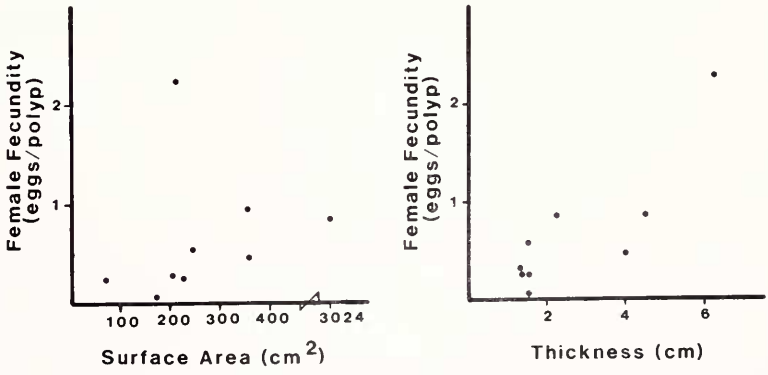

FIGURE 5. Female fecundity *versus* colony size and colony age. The fecundity of polyps in female colonies was significantly correlated with colony thickness (an estimate of minimum colony age) but was not correlated with the surface area of live colony tissues (colony size).

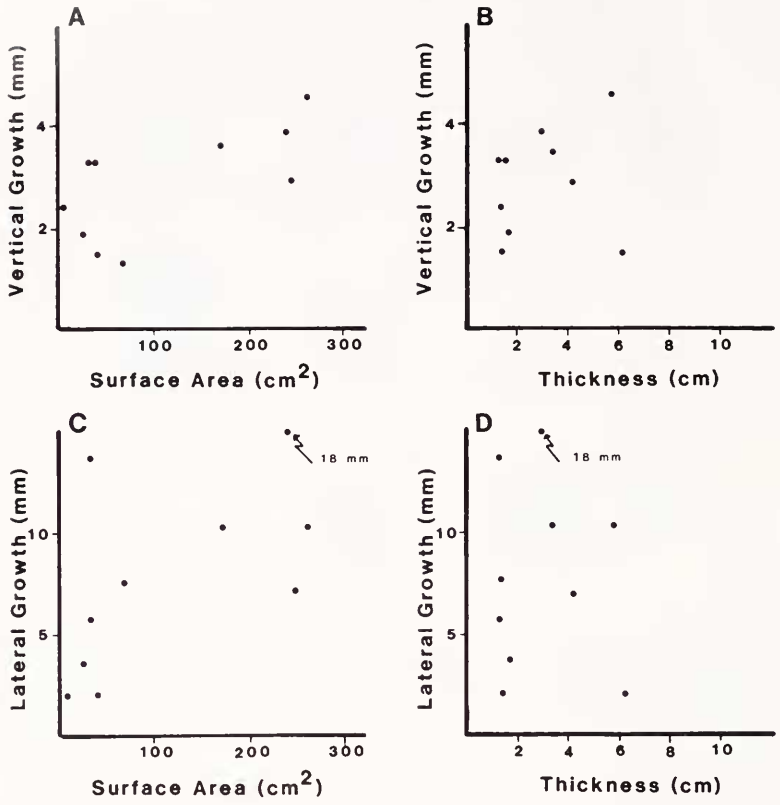

FIGURE 6. Colony growth *versus* colony size (surface area) and colony age (thickness). Vertical and lateral growth were both significantly correlated with colony surface area (A, C) and not with colony thickness (B, D).

and lateral (l) growth were significantly correlated with colony size ($r_{vs \cdot a} = .75$, $r_{ls \cdot a} = .67$, $P < .05$) (Fig. 6A, C). In contrast, partial correlations between vertical or lateral growth rate and colony age (thickness) were clearly not significant ($r_{va \cdot s} = -.3$, $r_{la \cdot s} = -.04$, $P > .05$) (Fig. 6B, D).

DISCUSSION

Periodicity of sexual reproduction

Sexual reproduction for the abundant Caribbean reef coral *Porites astreoides* occurs with both seasonal and lunar periodicities in Jamaica. Although some colonies contained gonads throughout the year, the proportion of reproductive colonies in the population and the fecundity of coral colonies varied seasonally. Colonies were maximally reproductive during the spring (April). Superimposed upon this annual pattern was a synchronized, lunar periodicity in the development of male gonads and larvae. Our data suggest male gametes are spawned prior to the full moon, and larvae are released around the time of the new moon. The lack of any clear lunar pattern in

the development of female gonads suggests that eggs may take more than a month to mature and/or may vary widely in developmental rate.

The subtle seasonal changes in coral reproduction described here (and elsewhere for other corals, *e.g.,* Harriot, 1983; Kojis and Quinn, 1984; Stoddart and Black, 1985) may have important implications for evaluating the annual reproductive activity of individual colonies. For example, variation among months in the frequency of reproductive colonies (Fig. 2) suggests that individual corals within a population may differ in the duration of their annual reproductive periods. In addition, seasonal differences in coral fecundity suggest that the fecundity of any given coral colony may vary throughout the year. Clearly, estimates of reproductive output based on observations at any single time of year or of only a few colonies would be misleading for this and, perhaps, other corals.

Breeding system

P. astreoides colonies are either female or hermaphroditic. This is the first description of a mixed breeding system of this type for corals—most appear to have predominantly unisexual (dioecious) or hermaphroditic (monoecious) colonies within a population (for reviews see Fadlallah, 1983; Harrison, 1985). It differs from Szmant's (1986) description of *P. astreoides* from Puerto Rico as simultaneously hermaphroditic, and is also in striking contrast to Indo-Pacific species of *Porites* that appear to be largely dioecious (Kojis and Quinn, 1982; Harriott, 1983; Harrison, 1985; Szmant, 1986) [although Kojis and Quinn (1982) did report a very low incidence of hermaphroditic colonies in the Pacific *P. andrewsi*].

The simultaneous occurrence of female and hermaphroditic colonies within a population might simply indicate that all colonies are potentially hermaphroditic, but male gonads have been missed in apparently female colonies due to a sampling error. However, the low probability of gender being misidentified from central tissues (1/54) suggests that *P. astreoides* having only female gonads within centrally located polyps contain only female gonads throughout the colony.

Alternately, female colonies might occur within a hermaphroditic population if gender varies seasonally or over a coral's lifespan, and, consequently, corals produce male gametes for only part of the time that they are reproductive (*e.g.,* Fadlallah, 1983). The temporally constant sex ratio in this population of *P. astreoides* (Fig. 2), however, suggests that seasonal shifts in gender are unlikely. Similarly, there does not appear to be a predictable change in gender associated with colony size and/or age (Rinkevich and Loya, 1979a, b; Kojis and Quinn, 1981). If colonies did switch from hermaphroditic to female with increasing size, the relative frequency of hermaphrodites would decline in larger size classes and the ratio of male to female gonads within hermaphroditic colonies should be negatively correlated with colony size. Neither are true for *P. astreoides.* Gender also does not appear to be a function of aging for *P. astreoides,* as both gender and the ratio of male to female gonads within hermaphroditic colonies were not associated with our estimate of colony age (thickness).

The combined results suggest, instead, that colonies of *P. astreoides* are either female or hermaphroditic and that hermaphroditic colonies are generally reproductive at smaller sizes than females (Fig. 4).

The apparent lack of true males within this population of *P. astreoides* suggests that there may be a reproductive disadvantage associated with making only male gametes (*e.g.,* Charnov, 1982). That is, individuals investing reproductive resources exclusively into male gonads would be less successful at producing offspring than

hermaphrodites. A mixed breeding system like that of *P. astreoides* might be selected for, for example, if the likelihood that sperm will fertilize eggs of another colony is unpredictable or temporally variable.

The unusual breeding system of *P. astreoides* also has important genetic implications. Some hermaphroditic corals are capable of self-fertilization (Kojis and Quinn, 1981; Heyward and Babcock, 1986). While cross-fertilization must occur in female colonies of *P. astreoides,* the proximity in hermaphroditic colonies of eggs and spermaries on some mesenteries suggests the potential for self-fertilization in this gender. If females and hermaphrodites of *P. astreoides* do differ in mode of fertilization, their respective offspring will also differ in genetic composition and diversity.

Ontogenetic changes and energetic constraints

Several life history features of *P. astreoides* appear to be under independent control; some are associated with colony size and others are associated with colony age (thickness). Moreover, it seems that the influence of at least colony size may differ between genders, as reflected by the difference between female and hermaphroditic colonies in the size at which most colonies become reproductive (Fig. 4).

When life history features of colonial animals, such as sexual maturity, are dependent upon colony size, they may vary as colonies grow or are reduced in size by external events (*e.g.,* Wahle, 1983, 1985; Hughes and Jackson, 1985; Kojis and Quinn, 1985; Szmant-Froelich, 1985; Karlson, 1986). For *P. astreoides,* reproductive state, vertical growth rate, and lateral growth rate are associated with colony size. Thus, these attributes potentially may change over a coral's lifespan as colony size increases or decreases.

Sexual reproduction and growth are often described as competing biological functions that draw on a limited supply of energetic or material resources within the individual (*e.g.,* Stearns, 1977). It has been predicted that rates of growth in colonial animals should decrease following the onset of sexual reproduction (Williams, 1975; Jackson, 1979; Kojis and Quinn, 1981). However, for *P. astreoides,* growth rates increase over the range of colony sizes associated with the onset of female reproduction (compare Figs. 4 and 6), suggesting that the presumed costs of gametogenesis do not result in a measurable depression of growth.

For female colonies of *P. astreoides,* polyp fecundity is associated with colony age (thickness) and not with colony size (Fig. 5). This suggests that polyp fecundity is a function of colony aging (*e.g.,* Kojis and Quinn, 1985). Thus total colony fecundity will be related both to the number of reproductive polyps within a colony and to colony age. The former often may be determined largely by colony size.

The lack of any correlation between fecundity and either size or age (thickness) among hermaphroditic colonies may reflect the difficulty of quantifying hermaphrodite fecundity. For example, there are different sampling biases inherent in estimates of egg *versus* spermary abundance from polyp cross-sections—because eggs and spermaries differ both in their distributions within mesenteries and in their potential residence times within coral polyps. Moreover, spermaries and eggs probably constitute quantitatively different investments of colony resources, contribute differently to the successful production of offspring, and thus cannot be compared directly. Such considerations will be important for accurately ranking or interpreting the fecundity of hermaphroditic colonies having different relative proportions of female and male gonads.

Patterns of gonad and larval abundance within individual colonies of *P. astreoides*

may reflect energetic and/or ontogenetic constraints. Low densities at colony edges might occur because the proximate allocation of colony resources to growth along the edge reduces the local resources available for gamete production (*e.g.,* Williams, 1975). Alternatively, lower fecundity along the edges of colonies might be an evolved "strategy" to ensure that valuable gonads are not located in colony tissues most likely to experience injury due to competition, predation, or growth into unsuitable habitats (*e.g.,* Jackson, 1979). Finally, if polyp fecundity is influenced by polyp age (Fadlallah, 1982; Wallace, 1985), higher fecundity in central polyps might simply reflect their relative age and stability. Although these three hypotheses are not mutually exclusive, we favor the last for *P. astreoides,* since it is consistent with the positive correlation observed between the fecundity of female polyps and colony age (thickness).

Conclusion

Patterns of sexual reproduction and growth described here for *P. astreoides* are complicated by the interaction of the following factors: (1) Temporal patterns of reproduction; (2) "pre-programmed" differences among colonies in fecundity apparently associated with aging; (3) size-related variation among colonies in reproductive condition and growth rate; and (4) differences between colony regions in fecundity. In large part, this complexity is related to the colonial mode of construction which allows reproductive activity to differ among polyps of a colony, and the life history features associated with size and age to vary independently.

ACKNOWLEDGMENTS

The comments of L. Hayek, H. B. McCarty, J. Render, C. M. Wahle, and an anonymous reviewer improved the manuscript. We thank C. M. Wahle for his valuable insight and criticism and for many stimulating discussions of colonial life histories, E. Sides for essential support and assistance in the field, P. P. Yevich for providing facilities for the histological preparations, R. Ramsay for help with field collections, and L. Hayek for consultation concerning statistical methods. This research was funded by grants to E.A.C. from the National Science Foundation (DEB 8105172) and Sigma Xi and by a research fellowship to E.A.C. from the Division of Biological Sciences of The University of Texas at Austin. Both authors were supported by Smithsonian Postdoctoral Fellowships during the final stages of this work. Publication #377 of the Discovery Bay Marine Laboratory, University of the West Indies.

LITERATURE CITED

ATODA, K. 1947. The larva and postlarval development of some reef-building corals. I. *Pocillopora damicornis c. espitosa* (Dana). *Sci. Reports Tohoku Univ. 4th Ser.* **18:** 24–47.

BABCOCK, R. C. 1984. Reproduction and distribution of two species of *Goniastrea* (Scleractinia) from the Great Barrier Reef Province. *Coral Reefs* **2:** 187–195.

BAK, R. P. M., AND M. S. ENGEL. 1979. Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Mar. Biol.* **54:** 341–352.

CHARNOV, E. L. 1982. *The Theory of Sex Allocation.* Princeton University Press, Princeton, NJ. 355 pp.

CONNELL, J. H. 1973. Population ecology of reef-building corals. Pp. 205–245, in *Biology and Geology of Coral Reefs, II. Biology,* O. A. Jones and R. Endean, eds. Academic Press, New York.

DODGE, R. E., S. C. WYERS, H. R. FRITH, A. H. KNAP, S. R. SMITH, C. B. COOK, AND T. D. SLEETER. 1984. Coral calcification rates by the buoyant weight technique: Effect of alizarin staining. *J. Exp. Mar. Biol. Ecol.* **75:** 217–232.

DUERDEN, J. E. 1902. West Indian madreporarian polyps. *Mem. Nat. Acad. Sci.* **8**: 401–597.

FADLALLAH, Y. H. 1982. Reproductive ecology of the coral *Astrangia lajolaensis* in a kelp forest habitat. *Oecologia* **55**: 379–388.

FADLALLAH, Y. H. 1983. Sexual reproduction, development and larval biology in scleractinian corals. *Coral Reefs* **2**: 129–150.

GLADFELTER, E. H., R. K. MONAHAN, AND W. G. GLADFELTER. 1978. Growth rates of five reef-building corals in the northeastern Caribbean. *Bull. Mar. Sci.* **28**: 728–734.

GOREAU, N. I., T. J. GOREAU, AND R. HAYES. 1981. Settling, survivorship and spatial aggregation in planulae and juveniles of the coral *Porites porites* (Pallas). *Bull. Mar. Sci.* **31**: 425–435.

GOREAU, T. F. 1959. The ecology of Jamaican reefs. I. Species composition and zonation. *Ecology* **40**: 67–90.

GOREAU, T. F., AND J. W. WELLS. 1967. The shallow-water scleractinia of Jamaica: Revised list of species and their vertical distribution range. *Bull. Mar. Sci.* **17**: 442–453.

HARRIGAN, J. 1972. The planula larva of *Pocillopora damicornis;* lunar periodicity of swarming and substratum selection behavior. Ph.D. thesis, University of Hawaii, 313 pp.

HARRIOTT, V. J. 1983. Reproductive ecology of four scleractinian species at Lizard Island, Great Barrier Reef. *Coral Reefs* **2**: 9–18.

HARRISON, P. L. 1985. Sexual characteristics of scleractinian corals: Systematic and evolutionary implications. *Proc. Fifth Int. Coral Reef Symp.* **4**: 337–342.

HARRISON, P. L., R. C. BABCOCK, G. D. BULL, J. K. OLIVER, C. C. WALLACE, AND B. L. WILLIS. 1984. Mass spawning in tropical reef corals. *Science* **223**: 1186–1189.

HEYWARD, A. J., AND R. C. BABCOCK. 1986. Self- and cross-fertilization in scleractinian corals. *Mar. Biol.* **90**: 191–195.

HIGHSMITH, R. 1982. Reproduction by fragmentation in corals. *Mar. Ecol. Prog. Ser.* **1**: 207–226.

HUGHES, T. P., AND J. B. C. JACKSON. 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission and fusion. *Science* **209**: 713–715.

HUGHES, T. P., AND J. B. C. JACKSON. 1985. Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.* **55**: 141–166.

JACKSON, J. B. C. 1979. Morphological strategies of sessile animals. Pp. 499–555 in *The Biology and Systematics of Colonial Organisms,* G. Larwood and B. Rosen, eds. Academic Press, New York.

JOKIEL, P. L., R. Y. ITO, AND P. M. LIU. 1985. Night irradiance and synchronization of lunar release of planula larvae in the reef coral *Pocillopora damicornis. Mar. Biol.* **88**: 167–174.

KARLSON, R. H. 1986. Disturbance, colonial fragmentation, and size-dependent life history variation in two coral reef cnidarians. *Mar. Ecol. Prog. Ser.* **28**: 245–249.

KINZIE, R. A., III, AND T. SARMIENTO. 1986. Linear extension rate is independent of colony size in the coral *Pocillopora damicornis. Coral Reefs* **4**: 177–181.

KOJIS, B. L., AND N. J. QUINN. 1981. Aspects of sexual reproduction and larval development in the shallow water hermatypic coral, *Goniastrea australensis* (Edwards and Haime, 1857). *Bull. Mar. Sci.* **31**: 558–573.

KOJIS, B. L., AND N. J. QUINN. 1982. Reproductive strategies in four species of *Porites* (Scleractinia). *Proc. Fourth Int. Coral Reef Symp.* **2**: 145–151.

KOJIS, B. L., AND N. J. QUINN. 1984. Seasonal and depth variation in fecundity of *Acropora palifera* at two reefs in Papua New Guinea. *Coral Reefs* **3**: 165–172.

KOJIS, B. L., AND N. J. QUINN. 1985. Puberty in *Goniastrea favulus* age or size limited? *Proc. Fifth Int. Coral Reef Symp.* **4**: 289–293.

LOYA, Y. 1976. The Red Sea coral *Stylophora pistillata* is an *r* strategist. *Nature* **259**: 478–480.

LUNA, L. G. 1968. *Manual of Histologic Techniques of the Armed Forces Institute of Pathology.* McGraw-Hill, New York.

MARSHALL, S. M., AND T. A. STEPHENSON. 1933. The breeding of reef animals part 1. The corals. *Sci. Rep. Great Barrier Reef Exp.* **3**: 219–245.

PETERS, E. C. 1984. A survey of cellular reactions to environmental stress and disease in Caribbean scleractinian corals. *Helgol. Meeresunters.* **37**: 113–137.

RINKEVICH, B., AND Y. LOYA. 1979a. The reproduction of the Red Sea coral *Stylophora pistillata,* I. Gonads and planulae. *Mar. Ecol. Prog. Ser.* **1**: 133–144.

RINKEVICH, B., AND Y. LOYA. 1979b. The reproduction of the Red Sea coral *Stylophora pistillata,* II. Synchronization in breeding and seasonality of planulae shedding. *Mar. Ecol. Prog. Ser.* **1**: 145–152.

RINKEVICH, B., AND Y. LOYA. 1985. Intraspecific competition in a reef coral: Effects on growth and reproduction. *Oecologia* **66**: 100–105.

ROGERS, C. S., H. C. FITZ, III, M. GILNACK, J. BEETS, AND J. HARDIN. 1984. Scleractinian coral recruit-

ment patterns at Salt River Submarine Canyon, St. Croix, U.S. Virgin Islands. *Coral Reefs* **3:** 69–76.

RYLAARSDAM, K. W. 1983. Life histories and abundance patterns of colonial corals on Jamaican reefs. *Mar. Ecol. Prog. Ser.* **13:** 249–260.

SHLESINGER, Y., AND Y. LOYA. 1985. Coral community reproductive patterns: Red Sea *versus* the Great Barrier Reef. *Science* **228:** 1333–1335.

SOKAL, R., AND F. ROHLF. 1969. *Biometry.* W. H. Freeman and Co., San Francisco. 776 pp.

STEARNS, S. 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Ann. Rev. Ecol. Sys.* **8:** 145–171.

STEELE, R. G. D., AND J. H. TORRIE. 1960. *Principles and Procedures of Statistics (with Special Reference to the Biological Sciences).* McGraw-Hill Book Company, Inc., New York. 481 pp.

STIMSON, J. S. 1978. Mode and timing of reproduction in some common hermatypic corals of Hawaii and Enewetak. *Mar. Biol.* **48:** 173–184.

STODDART, J. A., AND R. BLACK. 1985. Cycles of gametogenesis and planulation in the coral *Pocillopora damicornis*. *Mar. Ecol. Prog. Ser.* **23:** 153–164.

SZMANT-FROELICH, A. 1985. The effect of colony size on the reproductive ability of the Caribbean coral *Montastrea annularis* (Ellis and Solander). *Proc. Fifth Int. Coral Reef Symp.* **4:** 295–300.

SZMANT-FROELICH, A. REUTTER, AND L. RIGGS. 1985. Sexual reproduction of *Favia fragum* (Esper.): Lunar patterns of gametogenesis, embryogenesis and planulation in Puerto Rico. *Bull. Mar. Sci.* **37:** 880–892.

SZMANT, A. 1986. Reproductive ecology of Caribbean reef corals. *Coral Reefs* **4:** 43–54.

VAN MOORSEL, G. W. N. M. 1983. Reproductive strategies of two closely related stony corals (*Agaricia*, Scleractinia). *Mar. Ecol. Prog. Ser.* **13:** 273–283.

VAUGHAN, T. W. 1915. The geological significance of the growth-rate of the Floridian and Bahaman shoal-water corals. *J. Wash. Acad. Sci.* **5:** 591–600.

WAHLE, C. M. 1983. The roles of age, size and injury in sexual reproduction among Jamaican gorgonians. *Am. Zool.* **23:** 961.

WAHLE, C. M. 1985. Habitat-related patterns of injury and mortality among Jamaican gorgonians. *Bull. Mar. Sci.* **37:** 905–927.

WALLACE, C. C. 1985. Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. *Mar. Biol.* **88:** 217–233.

WILLIAMS, G. C. 1975. *Sex and Evolution.* Princeton University Press, Princeton, NJ. 200 pp.

WOOD-JONES. 1910. *Coral and Atolls.* Lovell Reeve & Co., LTD., London. 392 pp.